

## Revision of Two Prioniodontid Species (Conodonta) from the Early Ordovician Honghuayuan Formation of Guizhou, South China

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**ABSTRACT.** The septimembrate conodonts *Acodus triangularis* (Ding in Wang, 1993) and *Prioniodus honghuayuanensis* n.sp., are described and illustrated from Guizhou, South China where both species are widely distributed in Lower Ordovician strata. The adenticulate *A. triangularis*, which ranges through the middle and upper parts of the Honghuayuan Formation, is morphologically more primitive than the denticulate *P. honghuayuanensis*, which is present from the uppermost Honghuayuan Formation into the lower part of the succeeding Dawan Formation. *Prioniodus honghuayuanensis*, elements of which were previously ascribed to *Oepikodus communis* (Ethington & Clark, 1964), appears to be closely related to a species of *Prioniodus* from the basal Whiterockian of Utah, North America.

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Conodonts from the Honghuayuan Formation of Guizhou Province, South China were first studied by An (1987) in the Honghuayuan and Ganxi sections (Fig. 1). In the Honghuayuan section, An (1987) recognized three conodont assemblages with the lowermost consisting only of coniform species. The middle assemblage is characterized by the occurrence of *Serratognathus diversus* An, 1981. The upper assemblage is much higher in diversity, with the appearance of a number of pectiniform species of *Prioniodus*, *Bergstroemognathus* and *Rhipidognathus*. Similar faunas were also recorded from the Honghuayuan Formation of

Yanhe, northern Guizhou (An, 1987; X.Y. Chen *et al.*, 1995), and are widely distributed in the Honghuayuan Formation and age equivalent units in South China (An *et al.*, 1985; An, 1987; Wang, 1993).

More recently, conodont samples were collected from Lower Ordovician sections in Guizhou and other parts of South China with the aim of revising the faunas to provide support for a more precise biostratigraphic correlation and age alignment, both regionally and internationally. This revision will assist our understanding of the origin, radiation and phylogeny of the prioniodontid and related clades

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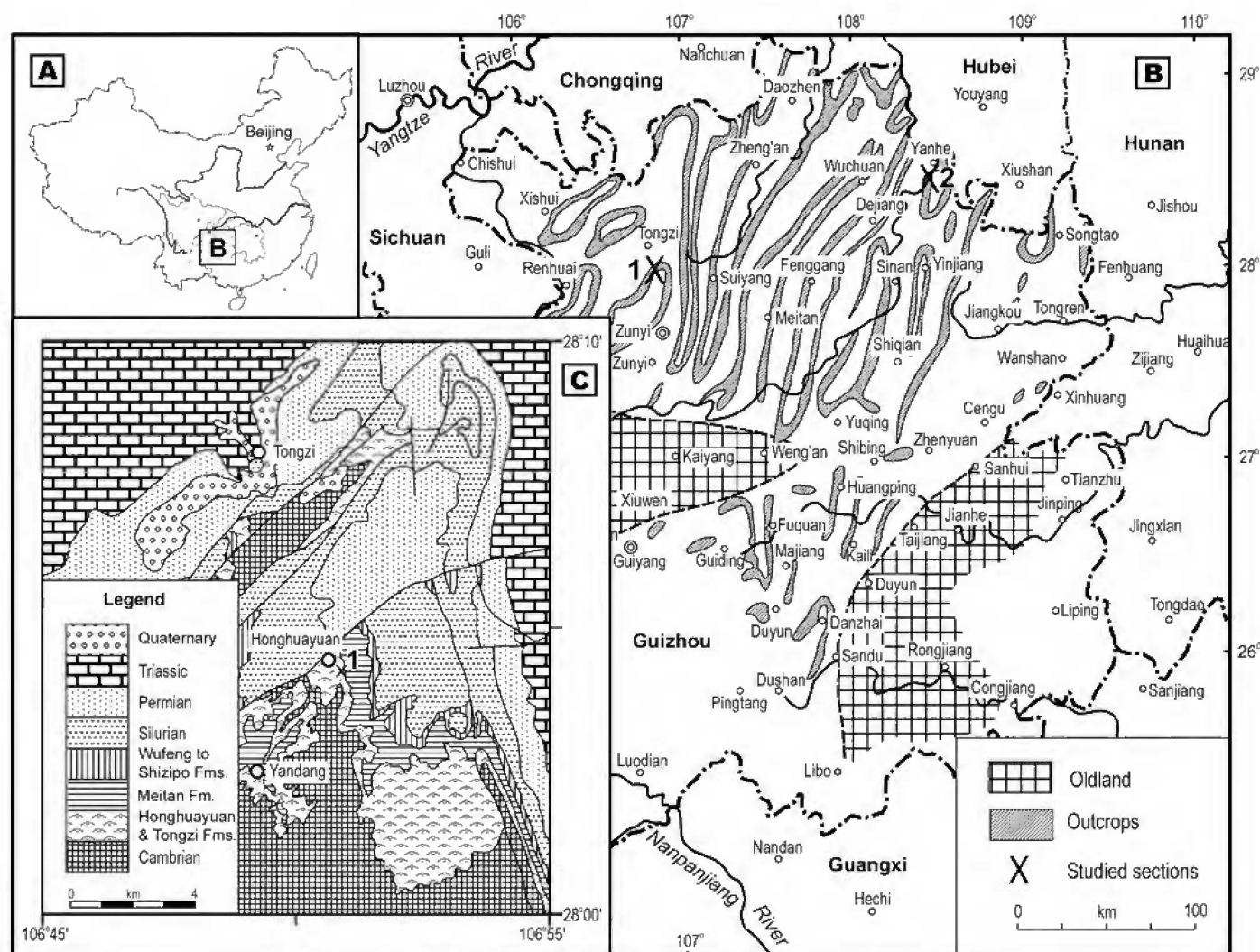


Fig. 1. Locality maps of the study areas. (A) China showing the location of Guizhou Province. (B) northeast Guizhou showing the distribution of the Ordovician rocks (after Gao, 1976) and the locations of two sampled sections for this study: 1) Honghuayuan Section of Tongzi; 2) Ganxi Section of Yanhe. (C) simplified geological map of the area in the vicinity of Honghuayuan village, showing the location of the Honghuayuan Section (Geology information modified from 1:200 000 Geology Map of Tongzi by Guizhou Regional Geological Survey, 1978).

through the late Early Ordovician. The present contribution is the first of several publications arising from this ongoing research project.

### Regional geological setting and lithostratigraphy

The Honghuayuan Formation was initially named the Honghuayuan Limestone by Chang & Sheng (1958) based on 40 m of grey, thick-bedded limestone at Honghuayuan, 7 km south of Tongzi County town, Guizhou (Fig. 1B,C). Zhang *et al.* (1964) renamed the unit the Honghuayuan Formation, which has been widely used to describe upper Lower Ordovician strata in South China (Wang *et al.*, 1996). The formation conformably overlies the Tongzi Formation. The contact with the overlying Meitan Formation is conformable and gradational (Fig. 1C).

The Honghuayuan Formation in the type section is a medium- to thick-bedded skeletal grainstone and packstone with thin-bedded to nodular skeletal wackestone (Fig. 2). Lime mudstone and shales are rare. Skeletal debris is mostly composed of cephalopods, brachiopods, trilobites, *Archaeoscyphia*, and bryozoans. The high biotic diversity suggests deposition in a well-circulated neritic environment.

Abundant skeletal grainstones and cross bedding indicate that the formation was mostly deposited in a shoreward environment in the high-energy, shallow subtidal zone (Fig. 2), although lower-energy, deep subtidal sediments, e.g., nodular argillaceous lime mudstone, are also present. Deposition of carbonates of the Honghuayuan Formation ceased due to sea level rise, to be replaced by an increasing supply of terrigenous muds, and then greyish green mudstone (the Meitan Formation) was deposited in Guizhou (Fig. 1C).

The Honghuayuan Formation is widely distributed in Guizhou (Fig. 1B) as well as on the Yangtze Platform with similar lithofacies in the Honghuayuan section (Wang *et al.*, 1996). Near shore facies of the formation deposited adjacent to eroded land (or island) areas are more dolomitic than the type section. Some patch reefs, which are mainly formed by abundant *Calathium* and less common *Archaeoscyphia* (Zhu *et al.*, 1995) were reported from the Huanghuachang section in Yichang, Hubei. The thickness of the Honghuayuan Formation on the Yangtze Platform is commonly 20 to 50 m, varying from a few metres to more than one hundred metres. In Guizhou, the thickness increases to more than 130 m northeastwards from the "Qianzhong Oldland" (an erosional land area at the time) (Fig. 1B).



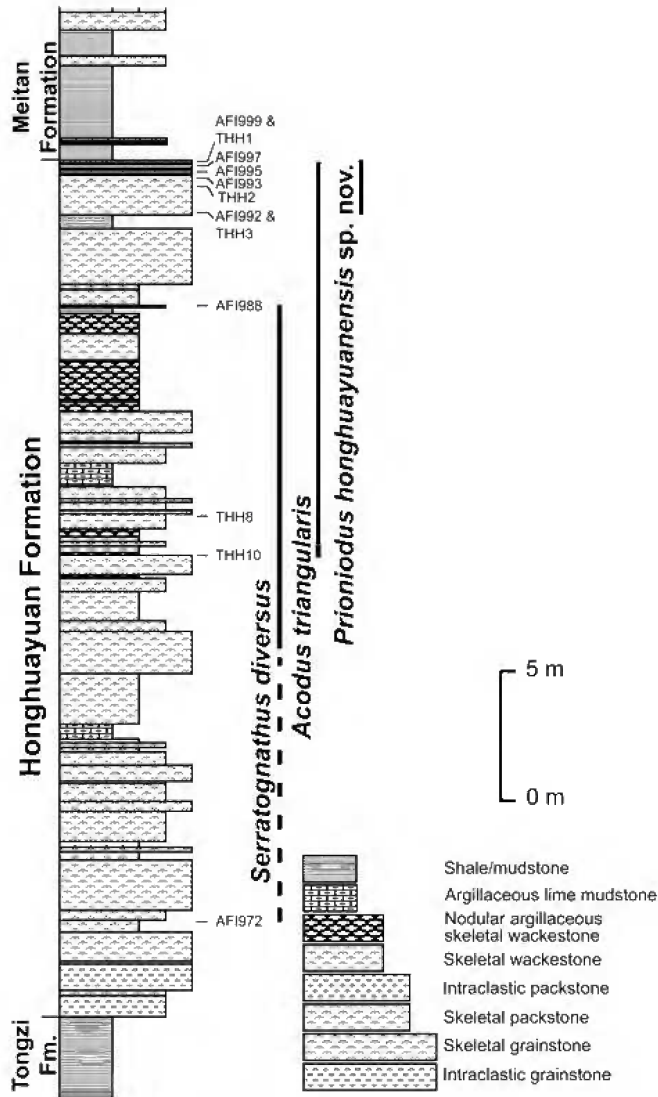


Fig. 2. Stratigraphic section through the Honghuayuan Formation at Honghuayuan, Tongzi, Guizhou Province showing the sampling positions and the stratigraphic ranges of *Serratognathus diversus* and the two species studied.

### Age and correlation of the Honghuayuan faunas

The most characteristic feature of the conodont faunas from the Honghuayuan Formation is the abundance of *Serratognathus diversus* in the middle part of the formation (Fig. 2). This distinctive conodont species is apparently restricted in distribution to South China, the Tarim Basin (Zhao *et al.*, 2000), and probably Australia (R.S. Nicoll, pers. comm.) and other biogeographically related tectonic units (Zhen *et al.* in Webby *et al.*, 2000; Zhen & Percival, 2003). An (1981, 1987) proposed the *S. diversus* Zone (divided into lower and upper subzones) based on the wide distribution of this species in South China, and correlated the lower subzone to the *P. proteus* Zone and the upper subzone to the *P. elegans* Zone of Baltoscandian successions. The *S. diversus* Zone was also approximately correlated with the *T. approximatus* graptolite Zone, evidenced by the occurrence of the *T. approximatus* fauna in deeper water clastic graptolitic facies laterally equivalent to the carbonate facies of the Honghuayuan Formation (X. Chen *et al.*, 1995).

An (1981, 1987) also recognized the *communis* Zone ranging from the top of the Honghuayuan Formation to the basal part of the overlying Dawan Formation in South China,

and correlated it with the *communis* Zone of North American Mid-continent successions. Although the age determination for the Honghuayuan Formation established by An (1981, 1987) is still current, the present study has demonstrated that the so-called "*Baltoniodus communis*" from South China of previous authors represents a new species of *Prioniodus*, *P. honghuayuanensis* named herein. It is neither conspecific nor congeneric with *Oepikodus communis* (Ethington & Clark, 1964), an index zonal species of North American Mid-continent successions. *Prioniodus honghuayuanensis* in fact exhibits close relationships with a younger unnamed species of *Prioniodus* from the basal Whiterockian succession of the Ibex area, Utah. The morphological changes (documented herein) from adenticulate *Acodus* species to denticulate *Prioniodus* indicate the likely origin of Prioniodontid clade. *Prioniodus honghuayuanensis* may have evolved from an adenticulate species revised herein as *Acodus triangularis* (Ding in Wang, 1993), which first occurs in the middle of the Honghuayuan Formation (THH10, Fig. 2) and is also associated with *P. honghuayuanensis* at the top of the Formation. Morphologically *Acodus triangularis* resembles *A. longibasis* McTavish, 1973 from the Emanuel Formation of Western Australia, which also represents the primitive adenticulate prioniodontid species, but is probably of slightly younger age.

### Material and methods

Twenty conodont samples (with prefix THH) were collected in 2000 from the Honghuayuan Formation in a 32 m thick limestone succession exposed on the hill slope to the southeast of Honghuayuan village (Fig. 1), about 10 km south of the Tongzi County. *Acodus triangularis* occurs in four samples (out of fifteen which yielded conodonts), whereas *Prioniodus honghuayuanensis* n.sp. was recovered from two samples at the top of the Formation (Table 1). All samples were completely dissolved in 10% acetic acid, with residues separated and concentrated using sodium polytungstate. Subsequently, 38 large samples (with prefix AFI) were recollected from the Honghuayuan Formation on this section (location coordinates: 28°04.27'N 106°50.91'E) to the southeast of the village. Both species were recovered from five samples at the top of the Honghuayuan Formation (Table 1).

In the Ganxi Section, measured along the road from Ganxi village to Shichangao, southwest of Yanhe County Town (Fig. 1, location coordinates: 28°22.72'N 108°25.70'E), the Honghuayuan Formation consists of 71.8 m of thick-bedded limestones. Out of 27 productive samples collected from this section (with prefix YTH), only one from the top of the Honghuayuan Formation yielded *Acodus triangularis* and *Prioniodus honghuayuanensis* (Table 1).

All photographic illustrations shown in Figs 3–9 are SEM photomicrographs captured digitally (numbers with the prefix IY are the file names of the digital images). Figured specimens bear the prefix AMF and are deposited in the collections of the Palaeontology Section at the Australian Museum in Sydney. Authorship of the new species is attributable solely to Zhen. Conodont terminology and notation employed in this contribution are conventional as defined in the Treatise Part W (Clark *et al.*, 1981), except for the M elements (makellate), whose orientation, morphology and terminology was introduced by Nicoll (1990, 1992).

**Table 1.** Distribution of *Acodus triangularis* and *Prioniodus honghuayuanensis* n.sp., in ten samples of the Honghuayuan Formation at the Honghuayuan Section of Tongzi, and in one sample from the top of the Honghuayuan Formation at the Ganxi Section of Yanhe, Guizhou Province, South China.

Samples	<i>Acodus triangularis</i>								<i>Prioniodus honghuayuanensis</i>								
	Pa	Pb	M	Sa	Sb	Sc	Sd	Total	Pa	Pb	?Pc	M	Sa	Sb	Sc	Sd	Total
AFI999	2	—	1	—	—	—	—	3	2	1	1	2	2	4	3	4	19
AFI997	13	5	6	5	4	2	7	42	9	4	—	7	13	12	11	16	72
AFI995	6	—	—	2	1	1	3	13	1	1	—	1	2	2	6	9	22
AFI993	26	26	18	7	2	3	11	93	34	11	—	38	26	53	27	103	292
AFI992	1	1	2	6	7	9	2	28	3	—	—	2	—	4	—	2	11
THH1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
THH2	—	—	4	1	—	—	—	5	—	—	—	—	—	—	—	—	—
THH3	5	4	2	3	2	2	4	22	—	—	—	1	1	—	—	1	3
THH8	1	1	—	—	—	—	1	3	—	—	—	—	—	—	—	—	—
THH10	4	—	1?	2	1	2	1	11	—	—	—	—	—	—	—	—	—
YTH1	1	—	—	—	—	1?	—	2	3	1	—	—	1	5	2	3	15
Total	59	37	34	26	17	20	29	222	52	18	1	51	45	80	50	138	435

**Systematic palaeontology****Class Conodonta Pander, 1856*****Acodus* Pander, 1856**

**Type species.** *Acodus erectus* Pander, 1856.

**Remarks.** The generic definition of *Acodus* and other related genera like *Tripodus* Bradshaw, 1969 and *Tropodus* Kennedy, 1980 has been a subject of disagreement among conodont workers (e.g., Lindström in Ziegler, 1977; Sweet, 1988, Kennedy, 1980; Albanesi in Albanesi *et al.*, 1998; Johnston & Barnes, 2000; X.H. Chen *et al.*, 2003). It seems likely that there are more than one genus involved in these species embraced under a rather broad definition of *Acodus* given by Zhen *et al.* (2004). However, a serious revision of this species group, which will certainly need a monographic treatment, is far beyond the scope of the present project, and the level of our current understanding of these species does not yet support such a major revision. *Acodus*, defined as a multielement genus by Lindström (in Ziegler, 1977), is deeply entrenched in the Ordovician conodont literature. It was widely distributed in the Early and Middle Ordovician, and played a crucial part in the origin and early evolution of several major pectiniform clades like prioniodontids and balognothids (Stouge & Bagnoli, 1999). We retain *Acodus* as a valid genus, although Pander's original specimens of the genotype, *A. erectus*, are irretrievably lost.

The type species of *Tripodus*, *T. laevis* Bradshaw, was originally defined as a form species on the basis of three specimens which show sharp anterior and posterior margins, a sharp blade-like costa on the outer lateral face situated more towards anterior margin, and a broad carina on the inner lateral face (Bradshaw, 1969). Based on material from the Ibex area of Utah, Ethington & Clark (1982) revised the type species of *Tripodus* as consisting of a quinque-membrate apparatus. This is interpreted herein as including geniculate M (oistodiform element, see Ethington & Clark, 1982, fig. 33A,B), alate triform Sa (trichonodelliform element, their fig. 33C), asymmetrical tetra-costate Sb (distacodiform element, their fig. 33F,G), asymmetrical laterally compressed Sc (drepanodiform element, their fig. 33H), and asymmetrical multi-costate Sd (paltodiform element, their fig. 33D,E) elements. Apparently the type

material of *T. laevis* would fall into the definition of the Sb element of the multi-element concept of the species, and the types of *Scolopodus alatus* Bradshaw, 1969, which Ethington & Clark (1982) regarded as part of the *T. laevis* apparatus, include both Sa (Bradshaw, 1969, pl. 132, fig. 4, paratype) and Sd (Bradshaw, 1969, pl. 132, figs 1–3, holotype) elements. Ethington & Clark (1982) also regarded *Triangulodus* van Wamel, 1974 as a junior synonym of their revised *Tripodus*. This raised the question as to whether *Tripodus* is likely a senior synonym of *Triangulodus* or a junior synonym of *Acodus*.

Based on material from western Newfoundland, Stouge (1984) regarded *Tripodus* as a junior synonym of *Acodus*, and suggested that *Acodus combsi* Bradshaw, 1969, *T. laevis* Bradshaw, and *S. alatus* Bradshaw represented different elements of one species apparatus which he called *A. combsi*. By assigning the prioniodiform P element represented by the form species *A. combsi* to the species apparatus, Stouge (1984) expanded the definition of *T. laevis* given by Ethington & Clark (1982), although at the time he was unaware of their work. Further differentiation of the prioniodiform Pa and Pb elements has completed the species apparatus as septimembrate (Albanesi in Albanesi *et al.*, 1998). Acodiform specimens assignable to the form species, *A. combsi* Bradshaw, 1969 were also reported from the Ibex area of Utah under the name "*Scandodus*" *robustus* Serpagli, 1974 (Ethington & Clark, 1982, pl. 10, fig. 25). This species definition for *T. laevis* has been more or less accepted by many Ordovician conodont workers (Sweet, 1988, Stouge & Bagnoli, 1988; Albanesi in Albanesi *et al.*, 1998; Bergström & Albanesi, 2001; Pyle *et al.*, 2003), although others (Johnston & Barnes, 2000; X.H. Chen *et al.*, 2003) retained the original concept of oistodiform M and costate S elements only as defined by Ethington & Clark (1982).

By taking *A. combsi* as the name bearer of the species, Stouge's work (1984) raised two questions: firstly, should *T. laevis* or *A. combsi* be the name bearer of the revised multi-element species, and secondly, to which genus should this species be assigned? In a recent documentation, Bergström & Albanesi (2001) reviewed the validity of the species name *Tripodus laevis*, and concluded that based on the most recent edition of ICZN rules, *T. laevis* is the valid name and *A. combsi* is a junior synonym of *T. laevis*. As for



the second question, some conodont workers follow Sweet (1988) in maintaining *Tripodus* as a valid genus and assigning *Acodus* as a *nomina dubia*, whereas others (e.g., Stouge & Bagnoli, 1988; Johnston & Barnes, 2000) utilize both *Acodus* and *Tripodus* by consigning species to the respective genus on historical reasons or on the details of the P and S elements. Based on the definitions of *Acodus* given by Lindström (in Ziegler, 1977) and of *Triangulodus* given by van Wamel (1974), both bear costate S and geniculate M elements, but *Acodus* has prioniodontiform (acodontiform) P elements instead of scandodontiform P elements without costa on lateral faces as in *Triangulodus*. However, as discussed above, the form species of *T. laevis* may represent the Sb element of the multi-element species apparatus adopted herein. If Stouge's (1984) revision of *T. laevis* is accepted, *Tripodus* is likely a junior synonym of *Acodus*. Ethington (pers. comm., 2004) suggested that the S elements of *Tripodus* were much more ornate in their surface morphologies than typical *Acodus* as demonstrated by *A. deltatus* Lindström, 1955 and *A. triangularis* Ding described herein, and the P elements of *T. laevis* (*A. combsi* s.f. of Bradshaw) were deeply albid with very shallow basal cavities and without prominent carinae on the cusps. Until the type species of *Tripodus* can be revised in detail the taxonomic relationship of these two genera remains uncertain.

In the type sections of the Marathon Basin of Texas, all three form species (*T. laevis*, *A. combsi* and *S. alatus*) were established based only on a few specimens, and *T. laevis* and *A. combsi* were not found in association (Bradshaw, 1969). Furthermore, co-occurrence of *Histiodelpha sinuosa* (Graves & Ellison) and *Periodon aculeatus* Hadding, 1913 in the Fort Peña fauna also suggests a younger age (Middle Ordovician, Yapeenian equivalent). Considering that the FAD (first-appearance datum) of *T. laevis* is a potential candidate for defining the base of the Middle Ordovician, detailed revision of this species at the type locality is urgently needed.

### *Acodus triangularis* (Ding in Wang, 1993)

Figs 3–5

?*Triangulodus* cf. *alatus* Dzik.—An *et al.*: 1985: pl. 8, figs 1, 4, 8.

?*Tripodus alatus* (Dzik).—An, 1987: p. 193, pl. 16, figs 3–6.

*Oistodus triangularis* Ding in Wang 1993: p. 185, pl. 19, figs 1, 2.

**Material.** 222 specimens from ten samples (Table 1).

**Diagnosis.** A species of *Acodus* consisting of a septimembrate apparatus including pastinate Pa and Pb, makellate M, triform alate Sa, triform asymmetrical Sb, modified cordylodiform Sc, and tetra-costate Sd elements; elements mostly albid and small in size, all bearing short adenticulate processes; P elements with a triangular base bearing a large, open basal cavity; S elements bearing a longer posterior process typically with a thin, blade-like crest along the upper edge.

**Description.** The pastinate Pa element has a reclined to suberect cusp and a large, triangular base (Fig. 3A–O). The cusp is triangular in cross section (Fig. 3F) with a sharp costa along the anterior and posterior margins, a mid-costa on the convex outer lateral face, and a smooth, more or less flattened inner lateral face. Three costae extend basally to merge with the upper margin of the anterior, posterior and

outer lateral processes respectively (Figs 3A,G,K,I,M, 4 O). Fine striations are best developed in the area posterior to the outer lateral costa on the outer lateral face (Fig. 3L). All three processes have a blade-like upper edge (Fig. 3E,G) and an expanded base with posterior and anterior processes extending in the same plane (Fig. 3H) or with anterior process slightly turned inner laterally (Fig. 3M–O). The outer lateral process extends basally and outer laterally in a direction nearly normal to the anteroposterior plane in upper or basal view (Fig. 3B,F), and is triangular in outline in anterior view (Fig. 3C,I) or posterior view (Fig. 3E). Posterior process extends posteriorly and typically longer than the other two (Fig. 3G,K). The anterior process is anticusp-like, triangular in outline in the lateral view (Fig. 3D,I–K). Basal cavity is pyramidal, large and moderately deep, with more or less straight basal margin or with both sides of the outer lateral process slightly restricted inward (Fig. 3B,H).

The Pb element is similar to the Pa element, but with a slightly proclined cusp (Fig. 4C,F,G,J,M), a shorter and less basally extended anterior process (Fig. 4A,B,G), a shorter and anterolaterally located outer lateral process (Fig. 4A,E,F,N), and a more open basal cavity (Fig. 4D,H). The side between the anterior process and the outer lateral process is less inwardly restricted, and the basal margins on both sides of the outer lateral process are less restricted inward in upper or basal view (Fig. 4B,D,E).

The M element is geniculate, anteroposteriorly compressed, with a low and well-developed outer lateral process and a short, anticusp-like inner lateral process, which is triangular in outline in anterior (Fig. 4K) or posterior view (Figs 3P, 4L). The anterior face is broadly convex and smooth, while the posterior face bears a broad carina and a weakly developed basal buttress. The basal margin is gently arched (Figs 3P, 4K,L).

The Sa element is triform and symmetrical with a robust cusp, a short adenticulate posterior process, and a blade-like adenticulate lateral process on the anterolateral corner of each side (Figs 4P–U, 5A). The cusp is isosceles triangular in cross section with a broad anterior face (Fig. 5A), a sharp costa along the posterior margin, and a sharp costa on each lateral side (Figs 4R,T, 5A). The three costae extend basally to form short, blade-like posterior and lateral processes (Fig. 4R,Q). Basal cavity is triangular in outline with moderate depth (Fig. 4R,U). Some specimens show a few small, rudimentary denticles along the thin upper edge of the posterior process (Fig. 4S).

The Sb element resembles the Sa element in being tricostate, but is distinguished by being markedly asymmetrical (Fig. 5B–J). The cusp is proclined, scalene triangular in cross section with a sharp costa along the anterior and posterior margins and a costa on the outer lateral face. The inner lateral face is concave and smooth or bearing a broad carina, with anterior margin prominently curved inwards (Fig. 5B,C,G). The outer lateral face is divided into a broadly convex area defined by the anterior costa and the outer lateral costa, and a gently concave area between the outer lateral costa and the posterior costa (Fig. 5D,F,H,I). The base is triangular in outline when posterior process is shorter (Fig. 5J), but in more advanced forms, it is strongly laterally compressed (Fig. 5E) as a long, adenticulate blade with a straight basal margin and a straight or weakly arched upper margin. The anterior process is anticusp-like, triangular in outline in the lateral view (Fig. 5I). The outer



Fig. 3. *Acodus triangularis* (Ding in Wang, 1993): (A–D) Pa element, AMF126732, AFI993, (A) outer lateral view (IY52005), (B) basal view (IY64002), (C) antero-outer lateral view (IY52007), (D) inner lateral view (IY64001); (E–G) Pa element, AMF126733, AFI993, (E) upper-posterior view (IY52003), (F) outer lateral view (IY52004), (G) upper view (IY52001); (H–K) Pa element, AMF126734, AFI993, (H) basal view (IY52009), (I) antero-outer lateral view (IY64005), (J) inner lateral view (IY52008), (K) outer lateral view (IY64003); (L–O) Pa element, AMF126735, THH8, (L) outer lateral view showing the fine striae in the area posterior to the outer lateral costa (IY64027), (M) antero-outer lateral view (IY64026), (N) outer lateral view (IY64025), (O) inner lateral view (IY59016). (P) M element, AMF126736, AFI992, posterior view (IY65034). Scale bars 100 µm unless otherwise indicated.

[Fig. 4 caption continued] ... (K,L) M element, AMF126740, AFI993, (K) anterior view (IY64009), (L) posterior view (IY52017). (M,N) Pb element, AMF126741, THH3, (M) outer lateral view (IY66032), (N) antero-outer lateral view (IY66034). (O) Pa element, AMF126742, THH10, outer lateral view (IY66037). (P–R) Sa element, AMF126743, AFI993, (P,Q) posterolateral views (IY66013, IY66014), (R) basal-posterior view (IY66012). (S–U) Sa element, AMF126744, AFI997, (S) lateral view (IY66010), (T) posterior view (IY66009), (U) basal view (IY66011). Scale bars 100 µm.





Fig. 4. *Acodus triangularis* (Ding in Wang, 1993): (A–E) Pb element, AMF126737, AFI992, (A) outer lateral view (IY53026), (B) upper view (IY53025), (C) inner lateral view (IY65016), (D) basal view (IY65017), (E) antero-outer lateral view (IY53027); (F,G) Pb element, AMF126738, AFI997, (F) outer lateral view (IY64010), (G) inner lateral view (IY52050); (H–J) Pb element, AMF126739, AFI993, (H) basal-inner lateral view (IY52011), (I) outer lateral view (IY64006), (J) inner lateral view (IY52010)... [continued p. 308]



Fig. 5. *Acodus triangularis* (Ding in Wang, 1993): (A) Sa element, AMF126745, AFI992, upper view (IY66022). (B–D) Sb element, AMF126746, AFI992, (B) basal-inner lateral view (IY65013), (C) inner lateral view (IY65012), (D) outer lateral view (IY53036); (E–H) Sb element, AMF126747, AFI992, (E) posterior view (IY53037), (F) antero-outer lateral view (IY65015), (G) basal-inner lateral view (IY53038), (H) outer lateral view (IY65014); (I) Sb element, AMF126748, AFI992, outer lateral view (IY65032); (J) Sb element, AMF126749, AFI992, outer lateral view (IY66029). (K, L) Sc element, AMF126750, THH10, (K) outer lateral view (IY66040), (L) inner lateral view (IY66041); (M) Sc element AMF126751, AFI992, inner lateral view (IY66027); (N) Sc element, AMF126752, THH3, upper view (IY66031); (O) Sc element, AMF126753, AFI992, inner lateral view (IY66026). ... [continued p. 311]



lateral process is also anticusp-like extending basally and outer-laterally with blade-like upper margin curved posteriorly. Basal cavity is moderately deep and triangular in outline and extends as narrow grooves underneath the posterior and anterior processes (Fig. 5B).

The Sc element is asymmetrical, strongly compressed laterally with a robust, proclined to suberect cusp, a posterior process varying from short (Fig. 5K,L) to relatively long (Fig. 5 O), and a short, anticusp-like anterior process (Fig. 5K–O). The cusp is convex lens-like in cross section, slightly bent inward with a sharp costa along its anterior and posterior margins, and with smooth outer and inner lateral faces, or with a weakly developed broad carina on the inner lateral face (Fig. 5 O). The inner lateral face is less convex with anterior margin gently curved inward. Basal cavity is convex lens-like in outline with gently arched basal margin in lateral view (Fig. 5M).

The Sd element is tetra-costate and asymmetrical, with a sharp costa along the anterior and posterior margins, and a sharp costa on each lateral side (Fig. 5P–AA). The outer lateral side is more convex with a broad convex area between the anterior process and the outer lateral process, and a less convex to concave area defined by the outer lateral process and the posterior process (Fig. 5P,U). The inner lateral side is less convex to concave with an inner laterally curved anterior margin (Fig. 5R,T,Y). Costae extend basally to merge with the upper margin of four corresponding short, blade-like processes. Small rudimentary denticles may occur along the upper edge of the posterior process of some specimens (Fig. 5P). However, the broken upper edge in some specimens superficially exhibits a denticulate appearance (Fig. 5U).

**Remarks.** *Oistodus triangularis* was originally proposed as a form species with the type material from the Honghuayuan Formation of Anhui Province (Ding in Wang, 1993). The two figured specimens are both pastinate with a large, triangular base and a robust cusp which bears a sharp costa along its anterior and posterior margins, and a third costa on the outer lateral face (Ding in Wang 1993, p. 185). The holotype has a reclined cusp and less downwardly extending anterior process (Wang, 1993, pl. 19, fig. 1), whereas the other figured specimen (Wang, 1993, pl. 19, fig. 2), with a suberect cusp and a longer and more downwardly extending anterior process, is identical with the Pa element described herein from Guizhou.

Specimens previously referred to *Triangulodus alatus* Dzik, 1976 from the lower Dawan Formation of South China (An *et al.*, 1985; An, 1987) possibly represent the S elements of *Acodus triangularis*. The type material of *T. alatus*, consisting of large-sized hyaline elements, occurs in late Darriwilian erratic boulders of NW Poland. The holotype (Dzik, 1976, p. 433, fig. 20k) is a scandodiform P element with an adenticulate posterior process and a short adenticulate anticusp-like anterior process. Dzik (1983, 1994) re-assigned this Baltic species to *Eoneoprioniodus*

Mound, 1965, which is likely a senior synonym of *Triangulodus* van Wamel, 1974 (see Clark *et al.*, 1981). *Triangulodus alatus* was also reported from the upper Darriwilian (*serra* Zone) of the Tarim Basin (Zhao *et al.*, 2000), and from the upper Darriwilian (*serra* Zone) of Oklahoma (Bauer, 1987).

Specimens referred to *Acodus deltatus* Lindström, 1955 from the Emanuel Formation of Western Australia (McTavish, 1973) are reassigned herein to *A. longibasis* which differs from *A. deltatus* mainly in having a more extended posterior process. This species from the Canning Basin shows some resemblance to *A. triangularis* from South China, in particular the Pa and S elements. Based mainly on the length of posterior process of the S elements in the Emanuel Formation, McTavish (1973) split this species into several subspecies of *A. deltatus* including *A. deltatus longibasis* McTavish with long posterior process, *A. deltatus deltatus* with a shortest posterior process, and *A. deltatus tortus* McTavish with an inwardly twisted cusp of the S elements. Similar variations are also observed in the species from South China with the posterior process of the S elements varying from short (Fig. 5J,L,K) to relatively long (Fig. 5B–H,M,O).

### *Prioniodus* Pander, 1856

**Type species.** *Prioniodus elegans* Pander, 1856.

**Remarks.** The type species of *Oepikodus* Lindström, 1955, *O. smithensis* Lindström, 1955, was originally proposed as a form species based on the oepikodiform elements (Lindström, 1955, pl. 6, figs 1–3). Subsequently, Lindström (1971) considered *Oepikodus* as a junior synonym of *Prioniodus*, 1856, and its type species, *O. smithensis*, along with *Oistodus longiramis* Lindström, 1955 to be parts of the revised multi-element species *Prioniodus evae* Lindström, which was also originally proposed as a form species based on the prioniodiform elements (Lindström, 1955, pl. 6, figs 4–10). Hence Lindström (1971) defined *P. evae* as consisting of a trimembrate apparatus including prioniodiform, oepikodiform and oistodiform elements. However, Bergström & Cooper (1973, pp. 323–324) pointed out that “the apparatus of *P. evae* differs from that of *P. elegans*”, the type species of *Prioniodus*, and “no element clearly homologous to the hibbardelliform element” existed in the latter. They further considered *Oepikodus* to be a subgenus of *Prioniodus*. This suggestion was formalized by Serpagli (1974). However, van Wamel (1974) and Lindström (in Ziegler, 1975) restored *Oepikodus* as a separate multi-element genus consisting of a trimembrate apparatus. Bergström (in Clark *et al.*, 1981) and Stouge & Bagnoli (1999) categorized *Oepikodus* and *Prioniodus* as belonging to different families.

Serpagli (1974) and Lindström (in Ziegler, 1975) redesignated the form species *P. evae* Lindström, 1955 as the type species of *Oepikodus*, since the originally

[Fig. 5 caption continued] ... (P–R) Sd element, AMF126754, AFI997, (P) outer lateral view (IY53002), (Q) posterior view (IY53001), (R) inner lateral view (IY53003); (S) Sd element, AMF126755, AFI997, basal-posterior view (IY66006); (T) Sd element, AMF126756, AFI997, inner lateral view (IY66001); (U,V) Sd element, AMF126757, AFI993, (U) outer lateral view (IY66017), (V) anterior view (IY66016); (W–Y) Sd element, AMF126758, THH3, (W) upper view (IY58017), (X) outer lateral view (IY58019), (Y) inner lateral view (IY58018); (Z,AA) Sd element, AMF126759, AFI993, (Z) inner lateral view (IY66018), (AA) posterior view (IY66020). Scale bars 100 µm.

designated type species *O. smithensis* became a synonym of *Prioniodus evae* (see Lindström in Ziegler, 1975, p. 237). As correctly pointed out by van Wamel (1974, p. 74), the form species *O. smithensis* is not a junior synonym of the form species *P. evae*, and the form species *O. smithensis* must therefore remain as the type species of *Oepikodus*. Although *O. smithensis* has page priority among the three form species erected by Lindström in the same publication for three different genera, they (*O. smithensis* Lindström, 1955, *P. evae* Lindström, 1955, and *Oistodus longiramis* Lindström, 1955) form the apparatus of a multi-element species, which was named as *P. evae* by Lindström (1971). With Lindström (1971) as the first reviser (see Article 24.2.2, ICZN of 1999 edition), *O. evae* (Lindström, 1955) emend. Lindström (1971) is recognized as a valid and proper name of the species with this multi-element apparatus.

Following the definition of *Oepikodus* as trimembrate (van Wamel, 1974) and then quadrimembrate (Bergström in Clark *et al.*, 1981), Stouge & Bagnoli (1988) suggested that *Oepikodus* consisted of a seximembrate apparatus that could be distinguished from *Prioniodus* by lack of the Sa element. Albanesi (in Albanesi *et al.*, 1998) concurred with this concept.

*Oepikodus*, as most recently revised by Nicoll & Ethington (2004), was defined as consisting of a septimembrate apparatus including pastinate Pa and Pb, makellate M and quadriramate S (Sa, Sb, Sc and Sd) elements. *Prioniodus* consists of a similar septimembrate apparatus that includes a triform alate Sa element, rather than a quadriform alate Sa element as in *Oepikodus*. Therefore, occurrence of the triform alate Sa element in the new species from the Honghuayuan Formation confirms its generic assignment to *Prioniodus*.

### *Prioniodus honghuayuanensis* n.sp.

Figs 6–8

*Baltoniodus communis* (Ethington & Clark).—An, 1981: pl. 4, figs 20–23, 25, 27–29, ?24.

*Baltoniodus communis* (Ethington & Clark).—An & Ding, 1985: p. 8, 9, pl. 1, figs 1–5, 8, ?9.

*Baltoniodus? communis* (Ethington & Clark).—An, 1987: p. 125, 126, pl. 19, figs 1–11.

*Baltoniodus communis* (Ethington & Clark).—Ding *et al.* in Wang, 1993: p. 161, pl. 23, figs 1–12.

**Etymology.** After Honghuayuan Village, where the type section of the Honghuayuan Formation is exposed on the hill slope located to the southeast of the village.

**Material.** 435 specimens, including holotype (AMF126760, from sample AFI993) and 19 paratypes (AMF126761–AMF126779), from eight samples (Table 1).

**Diagnosis.** Species of *Prioniodus* consisting of a septimembrate apparatus, including pastinate Pa and Pb elements with denticulate posterior and outer lateral process and adenticulate (or with rudimentary denticles) anterior

process which curves distally outer laterally; makellate M element with low but long inner lateral and outer lateral processes; alate triform Sa, triform asymmetrical (modified quadriramate) Sb, bipennate (modified quadriramate) Sc, and quadriramate Sd elements; all S elements with a proclined cusp, a long denticulate posterior process, and adenticulate (or rudimentarily denticulated) lateral and anterior processes.

**Description.** All elements are small, mostly albid, thin and fragile; the long denticulate posterior process of the P and S elements is broken in most specimens. Pastinate P elements bear a robust, laterally compressed cusp, with a sharp costa along its anterior and posterior margins, and with a prominent costa on the outer lateral face (Fig. 6). Surface of the cusp is ornamented with fine striation, which are best developed posterior to the outer lateral process on the outer lateral face (Fig. 6P). The posterior process is laterally compressed as a long blade with closely spaced, basally confluent, and more or less equal-sized denticles along its upper margin. The anticusp-like anterior process extends downward with its anterior margin strongly curved outwards and occasionally with confluent and small rudimentary denticles along its edge (Fig. 6F). The outer lateral costa extends downward to merge with the upper margin of the outer lateral process, which is long and bearing small, closely spaced denticles (Fig. 6B,M,N). The outer lateral process that extends downward laterally outward with an angle slightly  $>90^\circ$  (Pb, Fig. 6O) or nearly normal (Pa, Fig. 6D,G) to the posterior process is often broken in the present collection. Basal cavity is triangular in shape extending underneath the three processes as narrow grooves (Fig. 6E,F,Q,O). The Pa element has a suberect cusp with anterior process curved laterally outward and with the outer lateral process extending nearly normal to the posterior process in the upper view (Fig. 6D,G). The Pb element resembles the Pa, but with a reclined cusp and an inner-laterally bent posterior process (Fig. 6K–S).

The M element has a robust and strongly outer laterally reclined cusp, and adenticulate, low and long outer lateral and inner lateral processes (Fig. 7A–D). The cusp is slightly curved posteriorly and anteroposteriorly compressed, with a weak costa on the broad anterior face, and a broad carina on the posterior face. The outer lateral process has gently arched upper and basal margins, while the inner lateral process has nearly straight upper and basal margins. Basal cavity is relatively narrow, without prominent basal buttress (Fig. 7B,C).

The Sa element is triform and symmetrical with a proclined cusp, a long denticulate posterior process, and an anticusp-like lateral process on each side (Fig. 7E–S). The cusp is triangular in cross section with a broad anterior face (Fig. 7M, O), a sharp blade-like costa along the posterior margin, and a sharp costa along the anterolateral corner of each side (Fig. 7J, S). The posterior process is long, straight and strongly compressed laterally bearing small, closely spaced denticles (Fig. 7P–R). The blade-like costa on each side is gently curved posteriorly and extends basally to merge with the upper margin of the lateral process, which often bears rudimentary denticles (Fig. 7J,R). The basal cavity is an isosceles triangle in outline with moderate depth (Fig. 7E,J).

[Fig. 6 caption continued] ... AMF126762, (K) inner lateral view (IY63005), (L) outer lateral view (IY63006), (M) upper view (IY63007), (N) anterior view (IY63004), (O) basal view (IY50035), (P) close up of outer lateral view, showing the fine striae in the area posterior to the outer lateral costa (IY50036); (Q–S) Pb element, paratype, AMF126763, (Q) basal view (IY50027), (R) inner lateral view (IY63011), (S) outer lateral view (IY50028). All from sample AFI993; scale bars 100  $\mu\text{m}$  unless otherwise indicated.





Fig. 6. *Prioniodus honghuayuanensis* n.sp.: (A–E) Pa element, paratype, AMF126761, (A) antero-outer lateral view (IY50030), (B) basal-outer lateral view (IY50032), (C) outer lateral view (IY50033), (D) upper view (IY63010), (E) inner lateral view (IY63009); (F–J) Pa element, **holotype**, AMF126760, (F) basal view (IY50039), (G) upper view (IY63003), (H) outer lateral view (IY50038), (I) inner lateral view (IY63001), (J) postero-outer lateral view (IY50040). (K–P) Pb element, paratype, ... [continued p. 312]

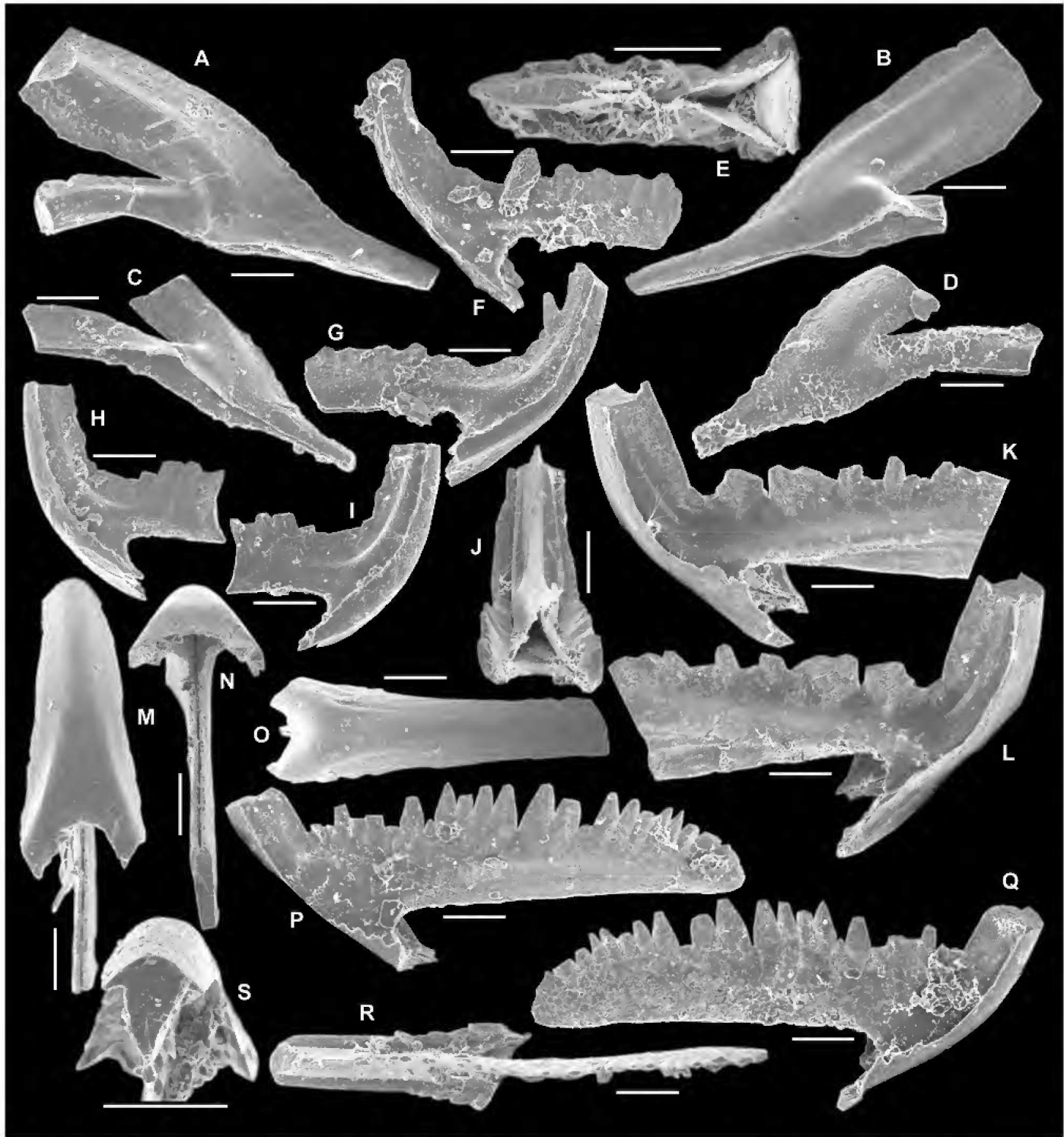


Fig. 7. *Prioniodus honghuayuanensis* n.sp.: (A,B) M element, paratype, AMF126764, AFI993, (A) anterior view (IY51011), (B) posterior view (IY63016); (C,D) M element, paratype, AMF126765, AFI993, (C) basal-posterior view (IY51015), (D) anterior view (IY63018). (E–G) Sa element, paratype, AMF126766, AFI993, (E) basal view (IY51003), (F,G) lateral views (IY51002, IY63012); (H,I) Sa element, paratype, AMF126767, AFI993, lateral views (IY63013, IY51005); (J–N) Sa element, paratype, AMF126768, AFI993, (J) basal-posterior view (IY51009); (K,L) lateral views (IY51010, IY51008), (M) anterior view (IY63014); (N) basal view (IY63015); (O) Sa element paratype, AMF126769, AFI993, anterior view (IY51006); (P–S) Sa element, paratype, AMF126770, AFI997, (P,Q) lateral views (IY51046, IY51048), (R) upper view (IY51045), (S) upper view showing the cross section of the cusp (IY63026). Scale bars 100  $\mu$ m.

[Fig.8 caption continued] ... AMF126774, AFI993, (I) inner lateral view (IY63021), (J) outer lateral view (IY51026), (K) basal view (IY51025); (L–P) Sc element, paratype, AMF126775, AFI997, (L) basal view (IY51050), (M) inner lateral view (IY51049), (N) outer lateral view (IY63028), (O) upper view (IY51051), (P) close up of the upper view showing the cross section of the cusp (IY51052); (Q) Sc element, paratype, AMF126776, AFI993, outer lateral view (IY51022). (R–T) Sd element, paratype, AMF126777, AFI993, (R) outer lateral view (IY63025), (S) inner lateral view (IY51037), (T) posterior view (IY51036); (U–X) Sd element, paratype, AMF126778, AFI993, (U) inner lateral view (IY63023), (V) outer lateral view (IY51033), (W) posterior view (IY51035), (X) postero-outer lateral view (IY51034); (Y–AA) Sd element, paratype, AMF126779, AFI993, (Y) postero-inner lateral view (IY51032), (Z) outer lateral view (IY63022), (AA) inner lateral view (IY51031). Scale bars 100  $\mu$ m unless otherwise indicated.





Fig. 8. *Prioniodus honghuayuanensis* n.sp.: (A–C) Sb element, paratype, AMF126771, AFI993, (A) inner lateral view (IY51013), (B) basal-inner lateral view (IY51014), (C) outer lateral view (IY63017); (D–F) Sb element, paratype, AMF126772, AFI993, (D) basal view (IY51020), (E) inner lateral view (IY51021), (F) outer lateral view (IY63020); (G,H) Sb element, paratype, AMF126773, AFI993, (G) inner lateral view (IY63019), (H) outer lateral view (IY51017). (I–K) Sc element, paratype, ... [continued p. 314]

The Sb element is strongly asymmetrical with a proclined and laterally compressed cusp, which bears a sharp costa along the anterior and posterior margins, and the third costa on the outer lateral face (Fig. 8A–H). The anterior costa is inner laterally curved and extends basally to merge with the upper margin of the anticusp-like downwardly extending adenticulate anterior process (Fig. 8A,E,G). The long posterior process is laterally compressed as a high blade bearing small, closely spaced denticles of similar sizes along its upper margin. The costa on the outer lateral face extends downward to merge with the upper margin of the downward extended, shorter, adenticulate outer lateral process. The inner lateral face is less convex, and bears a broad carina (Fig. 8A,B,E,G).

The Sc element is bipennate with a broad carina on each lateral face (more prominent on the inner lateral face), a short, adenticulate anterior process, and a long, laterally compressed, denticulate posterior process (Fig. 8I–Q). The cusp is proclined (Fig. 8Q), and laterally compressed with a sharp blade-like costa along its posterior and anterior margins (Fig. 8 O,P), which extends basally to merge respectively into the upper margin of the anterior process and the posterior process (Fig. 8I,M). The anterior process is anticusp-like, and curved laterally inward (Fig. 8I,M). The posterior process bears small, closely spaced denticles of more or less similar sizes (Fig. 8Q). The basal cavity is biconvex in outline, and extends as a narrow groove underneath the anterior and posterior processes (Fig. 8K,L).

The Sd element is quadriramate and asymmetrical, with an anterior process, a posterior process, and a lateral process on each side (Fig. 8R–AA). The cusp is proclined with a sharp blade-like costa along the anterior and posterior margins and on each lateral side (Fig. 8T,W,Y,AA). Anterior costa is inner laterally curved (Fig. 8S,U,Y), and extends basally to merge into the upper margin of the anticusp-like anterior process which is adenticulate or has small, fused rudimentary denticles along its distal edge (Fig. 8Y). As in the other S elements, the posterior process is long, laterally compressed, and blade-like bearing small, closely spaced denticles of similar sizes. The area defined by the anterior costa and the outer lateral costa is more broadly convex (Fig. 8R,V). The lateral costa on each side extends basally to merge respectively with the upper margin of the short inner and outer lateral processes. Both lateral processes extend downward and often bear small rudimentary denticles along their distal edges (Fig. 8S–U,W,X,AA).

**Remarks.** Although P elements of the new species show some resemblance to those of *Oepikodus communis* (Ethington & Clark, 1964), they differ in having denticulate outer lateral processes, and an anterior process which bears rudimentary denticles along its distal edge. The anterior process of *P. honghuayuanensis* extends strongly downward as an anticusp, and curves strongly outer laterally (Fig. 6F,J,Q). The Pb element of *O. pincallyensis* Zhen in Zhen *et al.*, 2003 has denticulate anterior, outer lateral and posterior processes, but the anterior process of the Pa element is adenticulate. However, the P elements of *O. pincallyensis* are distinctively curved inner laterally (Zhen *et al.*, 2003, fig. 19E,K) rather than outer laterally as in *P. honghuayuanensis* (Fig. 6D,M). Furthermore, the S elements of the new species can be easily distinguished from those of *O. communis*, *O. pincallyensis* and other species of *Oepikodus*. The Sa element is triform and alate with a

wide anterior face (Fig. 7M,O) and the open basal cavity is an isosceles triangle in outline (Fig. 7E,J). The Sb element can be described as asymmetrical triform (or modified quadriramate of some authors) with a strongly developed costa on the outer lateral face, which extends basally as a short but prominent adenticulate outer lateral process. The quadriramate Sd element of *P. honghuayuanensis* differs from that of *O. communis* in having more strongly developed costae, in having more prominent lateral processes, and in tending to develop rudimentary denticles along the distal edge of the anterior and lateral processes (Fig. 8S–U,W–Y,AA).

*Oepikodus communis* was originally proposed as a form species based on pastinate elements (Ethington & Clark, 1964). The type material shows a long denticulate posterior process with small, closely spaced denticles, and adenticulate anterior and outer lateral processes (Ethington & Clark, 1964, pl. 114, figs 6, 14, text-fig. 2F). Subsequently, Ethington & Clark (1982) revised *O. communis* in multielement taxonomy by accommodating another three form species which were reported in association with the type material of the form species *Gothodus communis* Ethington & Clark, 1964 in the El Paso Formation of Texas. These include *Oepikodus equidentatus* Ethington & Clark, 1964 with typical quadriramate ramiform elements (including symmetrical and asymmetrical), *Subcordylodus* sp. aff. *S. delicatus* (Branson & Mehl) with modified quadriramate ramiform elements (bearing only a weakly developed broad carina on the lateral faces), and *Oistodus longiramis* Lindström, 1955 comprising a makellate element with a long and slender outer lateral process. Ethington & Clark (1982) recognized the symmetry transition among the ramiform elements of four morphotypes, symmetrical quadriramate element, asymmetrical quadriramate element, modified quadriramate element with costa on one side, and modified quadriramate element without lateral costa. Therefore, they indicated a seximembrate apparatus for the species, although no formal notation was made. Repetski (1982) also suggested a seximembrate apparatus for *O. communis*, including prioniodiform, falodiform and four types of ramiform (belodiform, tetraprioniodiform, hibbardelliform, and cordylodiform) elements. Nicoll & Ethington (2004) defined *Oepikodus* as consisting of a septimembrate apparatus of a geniculate makellate M, four types of quadriramate or modified quadriramate S, and two types of pastinate P elements.

We also interpret *Oepikodus communis* as consisting of a septimembrate apparatus. The pastinate Pa element is represented by the holotype (Ethington & Clark, 1964, pl. 114, fig. 6) with a suberect cusp, and the pastinate Pb element by the other figured specimen of *G. communis* (Ethington & Clark, 1964, pl. 114, fig. 14) with a reclined cusp. The Sa and Sd elements are represented by the form species *O. equidentatus* Ethington & Clark (1964, pl. 113, figs 6, 8, 10, 11, 14). The Sa element is symmetrical or nearly symmetrical with a straight anterior margin, while the Sd element is markedly asymmetrical with a curved anterior margin (e. g. Ethington & Clark, 1964, pl. 113, fig. 14). The Sc element of *O. communis* is represented by those described and illustrated by Ethington & Clark (1964, p. 701, pl. 115, figs 1, 5, 7, 10) as *Subcordylodus* sp. aff. *S. delicatus* (Branson & Mehl, 1933). The makellate M element of *O. communis* is represented by those described and illustrated by Ethington & Clark (1964, p. 693, pl. 114, figs 2, 7) as *Oistodus longiramis* Lindström, 1955. The





Fig. 9. A–P, *Prioniodus* sp.: (A,B) Pa element, AMF126781, 100 feet above base of Kanosh Fm., Utah, (A) inner lateral view (IY66053), (B) upper view (IY66054). (C–E) Pb element, AMF126782, 83 feet above base of Kanosh Fm., Utah, (C) basal view (IY66051), (D) antero-outer lateral view (IY66052), (E) outer lateral view (IY66050). (F,G) Sd element, AMF126783, 78J-23, 150 feet above base of Juab Fm., Utah, (F) basal view (IY66061), (G) inner lateral view (IY66062). (H) Sa element, AMF126784, 78J-23, 150 feet above base of Juab Fm., Utah, lateral view (IY66060); (I–K) Sa element, AMF126785, 78J-16, top ledge of Wah Wah Fm., Utah, (I) antero-upper view (IY66042), (J,K) lateral views (IY66045, IY66043). (L) M element, AMF126786, 78J-16, top ledge of Wah Wah Fm., Utah, posterior view (IY66049). (M,N) Sb element, AMF126787, 100 feet above base of Kanosh Fm., Utah, (M) outer lateral view (IY66065), (N) inner lateral view (IY66066). (O) Sc element, AMF126788, 57 feet above base of Kanosh Fm., Utah, inner lateral view (IY66063); (P) Sc element, AMF126789, 78J-16, top ledge of Wah Wah Fm., Utah, outer lateral view (IY66047). (Q–U) *Prioniodus ?honghuayuanensis* n.sp.: ?Pc element, AMF126780, AFI999, (Q) inner lateral view (IY53012), (R) outer lateral view (IY65010), (S) upper view (IY53010), (T) outer-basal view (IY65008), (U) close up of outer lateral view showing fine striae in the area posterior to outer lateral costa (IY65009); Scale bars 100  $\mu$ m unless otherwise indicated.

asymmetrical Sb element is a modified quadriramate element with a more prominent costa on the outer lateral face (Albanesi in Albanesi *et al.*, 1998, pl. 6, fig. 22).

*Oepikodus intermedius* Serpagli, 1974, from the San Juan Formation of the Argentine Precordillera, is regarded herein as conspecific with *O. communis*; it was originally described as consisting of a trimembrate apparatus (prioniodiform, oistodiform and oepikodiform). In more recent revisions of the San Juan faunas, both Lehnert (1995) and Albanesi (in Albanesi *et al.*, 1998) did not recognize symmetrical Sa elements in any of the three species (*O. communis*, *O. intermedius* and *O. evae*) they ascribed to *Oepikodus*.

Lindström (in Ziegler, 1975) considered the form species *Gothodus microdentatus* van Wamel, 1974 from the Glauconitic Limestone of Sweden as part of *O. communis* species apparatus. However, not only have the well-recognized elements of *O. communis* apparatus not been recorded in association with this form species in Sweden, but also the triform, asymmetrical *G. microdentatus* shows rather different morphology in comparison with the ramiform elements of *O. communis* from North America. Based on the original description and illustrations (van Wamel, 1974), the form species *G. microdentatus* more likely represents the Sb element of a multi-element species of *Prioniodus* rather than of *Oepikodus*.

*Oepikodus communis* is widely distributed in North America (Ethington & Clark, 1964, 1982; Repetski, 1982; Stouge, 1982; Stouge & Bagnoli, 1988; Johnston & Barnes, 2000), Argentine Precordillera (Serpagli, 1974; Lehnert, 1995; Albanesi in Albanesi *et al.*, 1998), Australia (McTavish, 1973; Zhen *et al.*, 2003), and Greenland (Smith, 1991). However, as the result of inclusion of a triform alate Sa element in this species apparatus by An and other Chinese authors (An, 1981, 1987; An *et al.*, 1985; Ding *et al.* in Wang, 1993), the occurrence of *O. communis* in South China needs to be re-examined.

Specimens referable to the Pa, Pb, Sa, Sb, Sc and Sd elements of the present new species were first recorded from the top of the "Honghuayuan Formation" of Hexian, Anhui Province as *Baltoniodus communis* (An, 1981, 1987; An & Ding, 1985). An (1987) noted the abundant occurrence (up to 80% in some samples) of this species at the top of the Honghuayuan Formation in Guizhou, Hunan, Hubei and Anhui provinces, and correlated this interval at the top of the Honghuayuan Formation with the *communis* Zone of North America and with the *elegans* Zone of Baltoscandia. Although he recognized the occurrence of triform alate element as part of this species apparatus, An (1981, 1987) included this material into his rather broad interpretation of *O. communis* (Ethington & Clark, 1964). However, as the triform Sa element occurring in the material from South China had not been recognized at the type locality of *O. communis* in North America, An (1981, 1987) doubtfully assigned *O. communis* to *Baltoniodus* rather than *Oepikodus*.

Specimens previously referred to as aff. *Oepikodus? minutus* (McTavish, 1973) from the upper Wah Wah Formation, and the overlying Juab and Kanosh formations in the Ibex area of Utah (Ethington & Clark, 1982) somewhat resemble *P. honghuayuanensis*. Prof. R. Ethington kindly provided sixty specimens of this Utah species from nine samples for comparative study. Stratigraphically the Ibex species (designated herein as *Prioniodus* sp.; Fig. 9A–P) occurs at a slightly younger level

(basal Whiterockian, *victoriae* graptolite Zone) than the new species from South China. Similarities include the prioniodiform Pb element of *Prioniodus* sp. (Fig. 9C–E) that bears a denticulate outer lateral process with anterior margin curved outer laterally towards outer lateral process, and the ramiform S series that includes alate triform Sa (Fig. 9H–K), asymmetrical triform Sb (Fig. 9M,N), bipennate Sc (Fig. 9O,P), and quadriramate Sd (Fig. 9F,G) elements. However, the associated M element of the Ibex species shows a much shorter inner lateral process, and the Pa element has an adenticulate and weakly developed outer lateral process and a more or less straight anterior process. Bagnoli & Stouge (1997) referred this Ibex species to *Gothodus* Lindström, 1955. Based on the recent revision of *Gothodus* (Bagnoli & Stouge, 1997, and Stouge & Bagnoli, 1999), it has prioniodiform P elements comparable with those of *Oepikodus* and *Prioniodus*, but the S elements are more related to *Phragmodus* Branson & Mehl, 1933. However, most other conodont authors regard it as a junior synonym of *Prioniodus* (e.g., Bergström in Clark *et al.*, 1981) or *Baltoniodus* (Bagnoli *et al.*, 1988).

The new species from the Honghuayuan Formation shows some resemblance to *P. elegans* documented from Sweden by van Wamel (1974, p. 87–89, pl. 6, figs 1–6) and by Löfgren (1978, pl. 9, figs 1–6), but Swedish material of *P. elegans* has the M element with a denticulate inner lateral process and the P and S elements with better developed denticles on the lateral and anterior processes. *Prioniodus elegans* described from the Leningrad region of Russia and Tulubäcken of Sweden by Bergström (1988, pl. 3, figs 33–38), and from western Newfoundland by Stouge & Bagnoli (1988, pl. 13, figs 1–9) and Johnston & Barnes (2000, pl. 3, figs 1, 5–7, 11, pl. 16, fig. 17) has an even stronger development of denticulation with P elements bearing a longer, fully denticulated anterior process, and with S elements displaying well-denticulated anterior and lateral processes. The multi-element species definition of *P. elegans* followed herein conforms to the concept of Bergström (1971, 1981 in Clark *et al.*, 1981), van Wamel (1974), and Stouge & Bagnoli (1988). Stouge & Bagnoli (1988, p. 134) noted that this species displayed a large degree of morphological variation and might be polymorphic. Some of the material of *P. elegans* documented by Bergström (1988, pl. 3, figs 33–37) came from Popowka to the south of the Leningrad region, from where Pander's original type material (now lost) was collected. In comparison with those figured specimens of *P. elegans*, the P elements of *P. honghuayuanensis* display a more prominent cusp and smaller and less developed anterior and outer lateral processes (Fig. 6H,L), the P and S elements show less development of denticles on the anterior and lateral processes (Figs 6–8), and the M element lacks denticles on the inner lateral process (Fig. 7A–D). Also, the anterior process of the P elements in *P. elegans* is distinctively curved inner laterally (Bergström, 1988, pl. 3, fig. 33) rather than outer laterally (Fig. 6D,F,G) as in *P. honghuayuanensis*. In South China, *P. elegans* has only been recorded from the Jinshan Formation (biostratigraphically coeval with the Honghuayuan Formation) in Zhejiang Province of southeast China (An, 1987). It was also recorded from sub-surface core samples of the Tarim Basin, northwest China (Zhao *et al.*, 2000).

One specimen from the very top of the Honghuayuan Formation at the Honghuayuan Section (AFI999, Fig. 2) is



similar to the Pb element of *P. honghuayuanensis*, but is stellate in outline with an additional sharp, blade-like costa on the inner side of the cusp, which extends basally into a short process with a few small rudimentary denticles. It is tentatively referred to herein as a Pc element of *P. honghuayuanensis* (Fig. 9Q–U).

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